MEXICAN SPECIES OF THE GENUS *HETERANDRIA*, SUBGENUS *PSEUDOXIPHOPHORUS* (PISCES: POECILIIDAE)

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ABSTRACT.— The subgenus *Pseudoxiphophorus* is currently regarded as monotypic, with a single widespread species, *Heterandria bimaculata*, inhabiting the Atlantic slope of Middle America. Actually, the taxon includes two sharply distinct species in México, the more primitive being *H. jonesi*; other species of *Pseudoxiphophorus* occur in Guatemala. The basis for recognizing subgenera of *Heterandria* is presented as well as a detailed comparison between *H. bimaculata* and *H. jonesi*, including illustrations of gonopodia, gonopodial suspensoria, and the whole fish. *Heterandria jonesi*, which occurs at elevations up to 2,385 meters, is close to the ancestral stock of the genus.

RESUMEN.— El subgénero *Pseudoxiphophorus*, de acuerdo a la literatura corriente, es considerado como monotipico, con una sola especie de amplia distribución, *Heterandria bimaculata*, que habita la vertiente Atlantica de México y America Central. Como se muestra aqui, en México hay dos especies claramente distintas, la mas primitiva siendo *H. jonesi*; otras especies de *Pseudoxiphophorus* existen en Guatemala. La base para reconocer subgéneros de *Heterandria* se presenta asi como una comparacion detallada entre *H. bimaculata* y *H. jonesi*, incluyendo ilustraciones de gonopodios, suspensores de gonopodio, y ademas de el pez completo. *Heterandria jonesi*, que occure a alturas hasta 2.385 metros, es cercano a el tronco ancestral de el género.

Until the recent general review of the Poeciliidae by Rosen and Bailey (1963), *Heterandria* and *Pseudoxiphophorus* were regarded as monotypic genera represented, respectively, by *H. formosa* Agassiz in Florida and adjacent coastal lowlands, and by *P. bimaculatus* (Heckel) from northeastern México southward and eastward into Nicaragua. Among ichthyologists publishing on *Pseudoxiphophorus* during this century, only Regan (1904-1913) consistently maintained that this subgenus comprises two fully distinct species, although Hubbs (1924-1936) divided *P. bimaculatus* into four subspecies, including the one that is here restored to full specific status. Rosen and Bailey (1963: 131), commenting on Hubbs' action, indicated that the characters distinguishing these forms "are apparently clinal and grade imperceptibly from one race to another." In attempting to distinguish forms of *Pseudoxiphophorus*, overemphasis has been placed on the dorsal-ray number which varies widely in the two species of this group in México. As usual in poeciliids, the detailed architecture of the gonopodium proves to have far more important systematic value, although the size and position of the dorsal fin is also highly useful. Color pattern helps to distinguish the Mexican species (*Pseudoxiphophorus*) but it is too variable for complete reliance.

Regan was correct in concluding that *P. jonesi* (restricted to east-central México) and *P. bimaculatus* are distinct species, even though the male of *jonesi* was unknown to him. As here shown for the first time, the gonopodium of *Heterandria jonesi* is consistently and sharply distinct from that of *H. bimaculata*. Although these species have overlapping ranges they are rarely taken together, as in central Veracruz (see below). My paper on the zoogeography of Middle American freshwater fishes (Miller, 1966) did not include the extralimital *H. jonesi*, but recognition of more than one species of *Pseudoxiphophorus* in México was implied in the range statement for *Heterandria bimaculata*, since the subgenus *Pseudoxiphophorus* ranges northward into southeastern Tamaulipas.

This paper presents a detailed comparison between *H. jonesi* and H. *bimaculata* in México, illustrates their distinctive gonopodia and suspensoria as well as the general form and appearance of each species, and discusses variation in coloration, body proportions, and meristic characters. The distribution of the two species is also treated and support is presented for the view that *H. jonesi* is closest to the common ancestor of the genus.

SAN DIEGO SOC. NAT. HIST., TRANS 17(17): 235-250, 28 JUNE 1974

MATERIALS AND METHODS

Specimens examined came from the following museum collections: BMNH, British Museum (Natural History), P, Instituto Politecnico Nacional (México), UMMZ, University of Michigan Museum of Zoology, USNM, United States National Museum. I am grateful to P.H. Greenwood for making a syntype of *Mollienisia jonesii* available, to José Alvarez for the loan of topotypes of that species, to William M. McLane and Brandon McNair for information regarding the sympatric occurrence of *H. bimaculata* and *H. jonesi*, to Royal D. Suttkus for the loan and exchange of specimens, to the staff of the National Museum of Natural History (USNM) for facilities and working space, and to the John Simon Guggenheim Memorial Foundation for support as a Guggenheim Fellow while preparing this manuscript. Appreciation is also extended to Martha B. Lackey, former staff artist of the Museum of Zoology, for the accompanying illustrations, except Figure 4, drawn by Patricia J. Wynne, current staff artist. I am grateful to Mexican officials for permission to collect fishes in their country.

Table 1. Distinguishing characters of the subgenera of *Heterandria*.

Character	*Heterandria*	*Pseudoxiphophorus*
Gonopodium (Fig. 2):		
Serrae on posterior margin of ray 4p	7-9	9-18
Segments beyond distalmost serrae of ray 4p	5 or fewer	5 or more
Tip of ray 5a	Extends beyond tip of ray 4p	Extends to or falls short of of tip of ray 4p
Distal part of ray 3	Widely separated from ray 4	Closely adjoining ray 4
Gonopodial suspensorium (Fig. 3):		
Ligastyle	Reduced to an oval remnant below 10th vertebra	An elongate bone lying below 11th vertebra
Tip of gonapophysis I	Extends ventrally about 1/3 way from vertebral column to insertion of pelvic fin	Extends ventrally more than 1/3 to 1/2 way from vertebral column to insertion of pelvic fin
Reproductive biology:		
Superfetation	Strongly developed[1]	Absent as far as known
Egg size at fertilization, in mm[2]	0.37-0.40	2.08-2.56
Brood interval[3]	Averaging 5-6 days (small broods)	35-40 days (large broods)
Size	Minute; largest mature male ca. 14 mm S.L.	Moderate; smallest mature male (*jonesi*) ca. 22 mm S.L.
Dorsal fin of female	About equal in size to anal, its origin behind anal origin, over 16th or 17th vertebra	Much larger than anal, its origin usually farther forward (behind in one species), over 12th to 15th vertebra[4]
Dorsal rays	6-8	9-18
Vertebral number	Sexually dimorphic; males 32-34, females 30-33 (Table 4)	No sexual dimorphism; total variation, 30-34

[1]As many as 6 stages of developing embryos in a single ovary (Turner, 1937).
[2]From Scrimshaw, 1946; based on *H. formosa* and *H. bimaculata* only.
[3]At height of reproductive season (Turner, 1937).
[4]Over 16th in one form in Alta Verapaz, Guatemala (D.E. Rosen, pers. comm.)

Counts and measurements were made as prescribed by Hubbs and Lagler (1958: 19-26). Measurements are expressed as permillages of the standard length; they were taken with dial calipers reading to the nearest tenth of a millimeter. One ratio (length of depressed dorsal into predorsal length) was stepped off with a pair of dividers and estimated to the nearest tenth. A second ratio (base of dorsal fin into predorsal length) was measured with calipers, converted into permillages, and mathematically calculated—a more accurate and objective means of obtaining the required figures. The vertebral count includes the hypural plate as the terminal vertebra; the second vertebra is the first rib-bearing one in all cyprinodontoids.

CHARACTERS OF THE TWO SUBGENERA

When only two species were assigned to *Heterandria*, the need for subgeneric recognition was minimal. Now that *Pseudoxiphophorus* is polytypic (probably containing three or more species—Miller, 1966, and Rosen and Bailey, MS), it is helpful to employ the subgenus when discussing the Middle American forms. Consequently I have drawn up a comparison (Table 1) which provides a biological as well as a structural basis for recognizing two subgenera of *Heterandria;* some may feel the differences are sufficient for generic recognition. Characters that indicate a close relationship between *Pseudoxiphophorus* and *Heterandria* involve the morphology of the reproductive system and the breeding behavior as well as the osteology of the skull (as pointed out by Rosen and Bailey, 1963: 128-129). Another interesting common feature discovered in the present study is the marked sexual dimorphism in the length of the snout: *H. jonesi*—43 males, 78-96; 47 females, 92-111. *H. bimaculata*—30 males, 82-100; 30 females, 94-111. (Figures are permillage of standard length; see Table 3.) *H. formosa*—10 males, 58-75; 10 females, 76-89. Another interesting aspect of the comparison is the sexual dimorphism in vertebral number in subgenus *Heterandria* only: males, 32 (8), 33 (26), 34 (3); females, 30 (1), 31 (13), 32 (18), 33 (1)—Table 4. The tiny egg of the subgenus *Heterandria* is correlated with the high degree of dependence on the mother for nourishment by the developing embryo. Such virtual elimination of yolk is paralleled in certain species of *Poeciliopsis* (e.g., *Poeciliopsis elongata* [Günther] and *P. prolifica* Miller—see Schultz and Thibault, MS), in which superfetation is also strongly developed. Presumably superfetation is not developed in subgenus *Pseudoxiphophorus* (checked only in *H. bimaculata* and *H. jonesi*).

THE MEXICAN SPECIES

Heterandria jonesi (Gunther)
(Figs. 1-3)

Mollienisia jonesii.— Günther, 1874: 371 (original description, based on females only; Lago Alcuhuaca, México = Lago de Aljojuca — see Alvarez, 1950).

Gambusia jonesii.— Regan, 1907: 260 (name; comparisons). Regan, 1906-08: 94, 97-98, pl. 12, fig. 8 (key; description; synonymy; female syntype figured; distribution).

Pseudoxiphophorus jonesii.— Regan, 1913: 993 (synonymy; description; range).

Pseudoxiphophorus bimaculatus jonesii.— Hubbs, 1924: 17-18 (characters; synonymy). Alvarez, 1950: 88-91 (redescription of topotypes; correction of type locality to Lago de Aljojuca, 15 km NE of Ciudad Cerdán, Puebla; comparison with sample from Tepeaca, Puebla, in Río Balsas basin).

Pseudoxiphophorus bimaculatus (misidentification).— Woolman, 1894: 55-56 (description; Río Blanco at Orizaba). Jordan and Evermann, 1896: 678 (description, based on Orizaba specimens). Meek, 1904: 127 (in part; Orizaba records only).

Heterandria bimaculata (misidentification).— Rosen and Bailey, 1963: 131 (in part; references to *jonesi* and *pauciradiatus*).

Pseudoxiphophorus reticulatus (misidentification).— Jordan and Evermann, 1896: 678, footnote (description of specimens from Río Blanco at Orizaba, where only *H. jonesi* occurs).

Pseudoxiphophorus pauciradiatus.— Regan, 1904: 256 (original description, based on 8 of Woolman's specimens from Orizaba). Regan, 1905: 362-363 (validity of species; comparison with *bimaculatus*). Regan, 1907: 260 (listed as synonym of *Mollienisia jonesii*).

Diagnosis.—A species of the subgenus *Pseudoxiphophorus* (Table 1) distinguished from *H. bimaculata* as follows (see also Table 5): Terminal segment of ray 4a of gono-

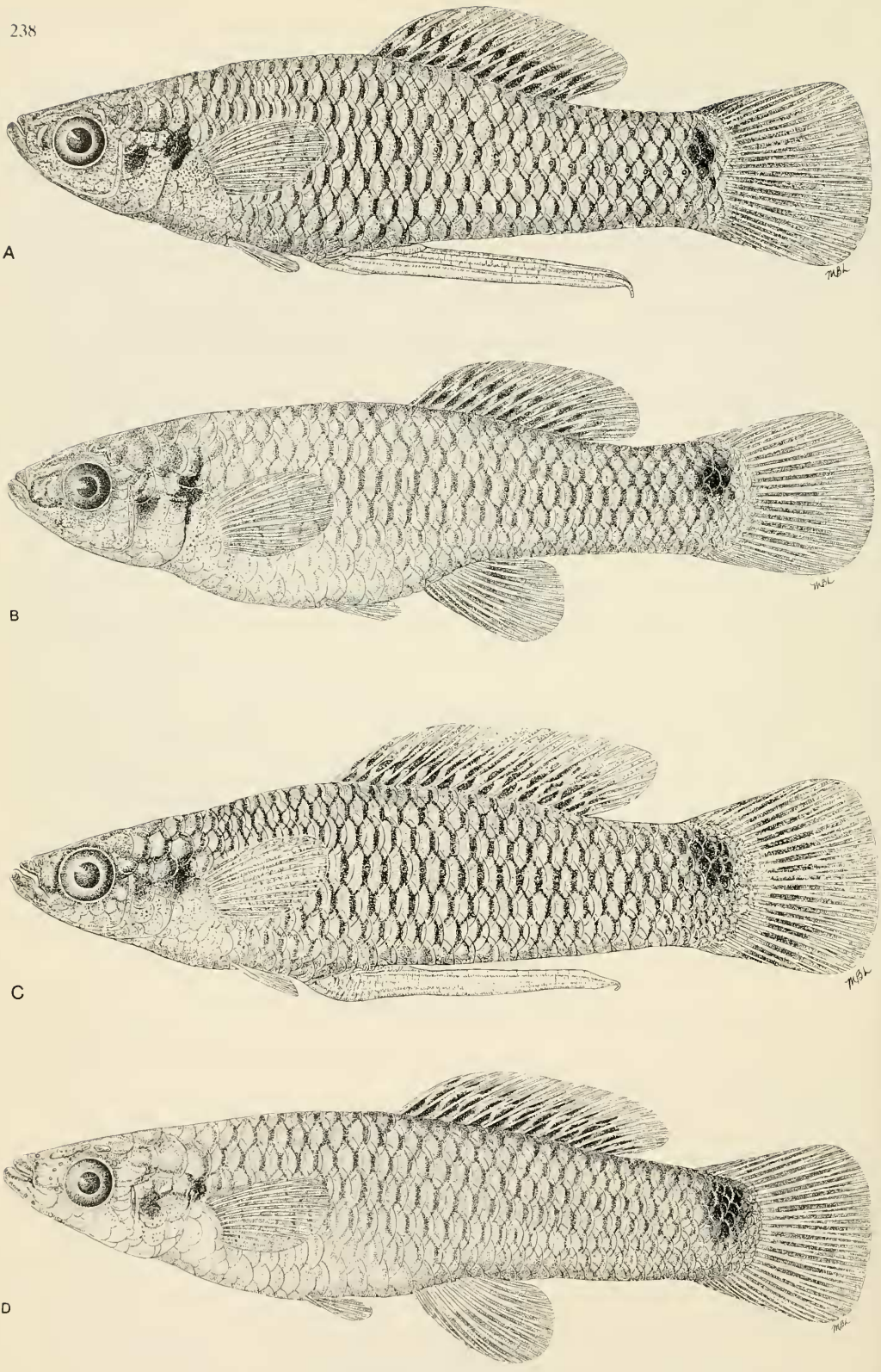

Figure 1. Top to bottom: *Heterandria jonesi*, adult male, 37 mm, Rancho Sierra de Agua, Orizaba Valley (UMMZ 183894); *Heterandria jonesi*, adult female, 43.5 mm, from same collection (topotypes of *P. pauciradiatus* Regan); *Heterandria bimaculata*, adult male, 35.5 mm, Nacimiento de Cosolapa (UMMZ 183902); *Heterandria bimaculata*, adult female, 50 mm, from same collection.

podium short (not longer than 2-3 subdistal segments and often barely exceeding penultimate one), slightly recurved, not reaching tip of enclosing membrane; anterior margin of subdistal segments of ray 4a smooth; ray 4p forming part of curved tip of gonopod (Fig. 2). Base of dorsal fin enters predorsal length 1.6 to 2.4 times in males, and 2.0 to 2.9 times in females; depressed dorsal fin enters same distance 1.2 to 1.6 (rarely 1.1) times in males, and 1.4 to 2.0 times in females. Origin of dorsal fin more posterior (Table 3). Basicaudal spot generally smaller, lower, and more anterior, lying mostly on caudal peduncle.

Type locality.—This species was described from Lago de Aljojuca, a crater lake or *axalapazco* (Tamayo, 1964: 113) in the endorheic part of the high Puebla Plateau (Llanos de El Salado), 15 km northeast of Ciudad Cerdán, Puebla, and west of the great volcano Pico de Orizaba (5,750 m) at an elevation of 2,385 m (Alvarez, 1950, 1972). Apparently it is the only fish native to this lake, although three other similar lakes to the north each

Table 2. Variation in number of dorsal fin rays in two species of *Heterandria* from México.

Cat. no. and/or authority and locality[1]	Number of dorsal rays									No.	Avg.
	9	10	11	12	13	14	15	16	17		
H. jonesi											
P 203, Alvarez, 1950 (topotypes)[2], Lago de Aljojuca, Puebla	–	–	70	34	–	–	–	–	–	104	11.33
P 184, Tepeaca, Puebla (Balsas basin)	–	–	6	13	1	–	–	–	–	20	11.75
183986, Acosac, Puebla (Balsas basin)	–	–	17	13	–	–	–	–	–	30	11.43
186675, Tehuacán, Puebla (Papaloapan basin)	–	–	1	22	7	–	–	–	–	30	12.20
183894, Hubbs, 1924, 1926, Orizaba Valley	–	–	38	149	14	7	3	–	–	211	12.00
162143, Río Atoyac, Veracruz[3]	1	3	48	43	1	–	–	–	–	96	11.42
183896, Río Atoyac, Veracruz	–	–	96	29	–	–	–	–	–	125	11.23
124304, Río Necaxa, Puebla (Tecolutla basin)	–	–	–	24	20	3	–	–	–	47	12.55
193493, 42 km WSW Poza Rica, Veracruz (Cazones basin)	–	–	1	12	5	1	–	–	–	19	12.32
124330, 162141, Palitla, S.L. Potosí (Pánuco basin)	–	–	–	19	54	3	–	–	–	76	12.79
183887, Jaumave, Tamaulipas (Tamesí basin)	–	–	–	–	8	24	3	–	–	35	13.86
H. bimaculata											
Hubbs, 1924, 1926, Jico and Jalapa, Veracruz (Chachalacas basin)	–	–	–	2	30	11	2	–	–	45	13.29
USNM 31023, 45489, Mirador, Veracruz (Chachalacas basin)	–	–	–	–	6	23	4	–	–	33	13.94
162144, Río Atoyac, Veracruz[4]	–	–	–	–	8	26	4	–	–	38	13.89
181309, Hubbs, 1924, 1926, Córdoba, Veracruz (subtopotypes)	–	–	–	1	7	30	13	–	–	51	14.08
Regan, 1905, Río Tonto, Veracruz (Papaloapan basin)	–	–	–	–	–	5	7	3	–	15	14.87
183902, Cosolapa, Oaxaca (Papaloapan basin)	–	–	–	3	12	32	13	–	–	60	13.92
124234, 4 km E El Hule, Veracruz (Papaloapan basin)	–	–	–	3	21	28	1	–	–	53	13.51
Regan, 1905, in Hubbs, 1924, Sto. Domingo Petapa, Oaxaca (Coatzacoalcos basin)	–	–	–	–	–	1	3	1	1	6	15.33
178533, Río Sarabia, Oaxaca (Coatzacoalcos basin)	–	–	–	–	–	12	23	16	–	51	15.08

[1]Catalog numbers are those of UMMZ unless otherwise stated.
[2]In 28 loaned from this series I counted 11 (22), 12 (6). Also included is a count of 12 on a syntype, BMNH 1873.1.13.1 (illustrated by Regan, 1906-08: Pl. 12, Fig. 8).
[3]Sympatric with *bimaculata* (162144).
[4]Sympatric with *jonesi* (162143).

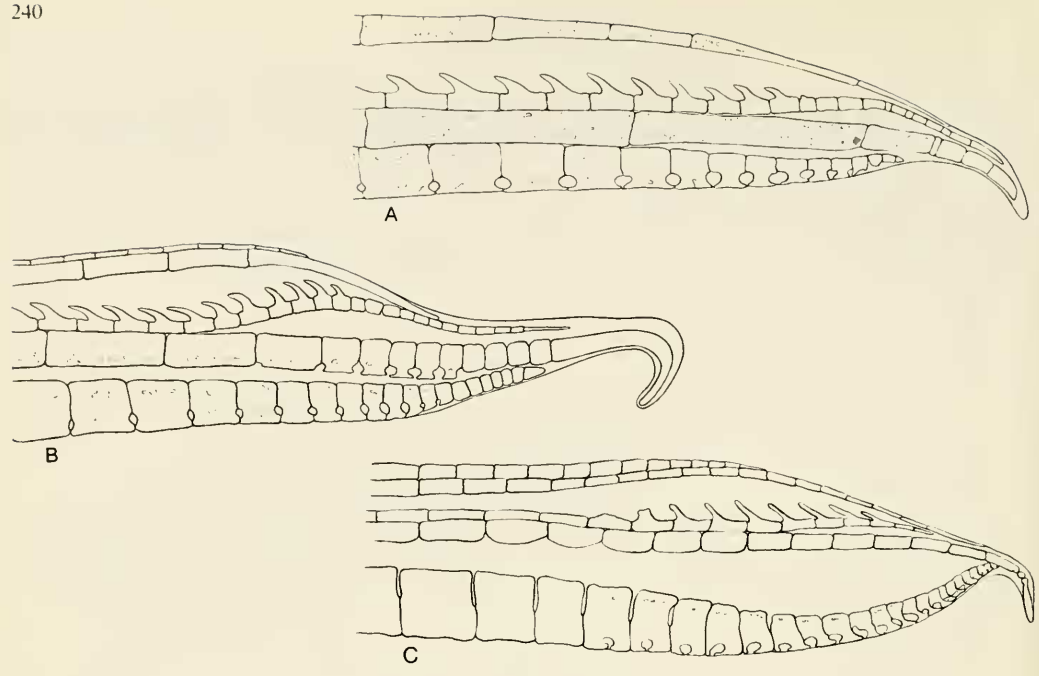

Figure 2. Gonopodia of: A. *Heterandria jonesi*; B. *Heterandria bimaculata*; C. *Heterandria formosa.*

contain an atherinid of the genus *Poblana* (=*Chirostoma;* see Bolland and Barbour, MS). The fish was named for its discoverer, T.M. Rymer Jones.

Variation.—The gonopodium (Figs. 2, 3) provides the major criterion for distinguishing *H. jonesi* from its relatives. It is therefore important to know how much it varies. The three characteristics given in the diagnosis include the variation known for the populations examined. Other features follow. Ray 3 terminates near the proximal end of segments 3 to 6 of ray 4a. There is sharp transition between the several elongate proximal segments of ray 4a and the short subterminal segments. There is always a rather abrupt change in height and size between the most proximal serra-bearing segment of ray 4p and the next succeeding segments of this ray. These shorter segments, which precede the last one of ray 4a, vary from 2 to 5. Ray 4p has from 12 to 18 strong, retrorse serrae. Ray 5a ends about 2 to 4 segments from the tip of ray 4a.

Ten measurements were made on males and females of four populations of *H. jonesi* (Table 3) representing: (1) the type locality of the species (Aljojuca), at 2,385 m; (2) the type locality of *P. pauciradiatus* (Orizaba), at 1,240 m; a locality (Palitla) in the southern part of the Río Pánuco basin, at about 120 m; and the northernmost known population (Jaumave), in the headwaters of the Río Guayalejo, at about 330 m. These data show that: (1) Aljojuca and Orizaba specimens have the shortest dorsal-fin base, Jaumave the longest, with Palitla intermediate; (2) Jaumave females have the longest anal fin, Orizaba and Aljojuca the shortest, with Palitla somewhat intermediate; (3) the caudal fin is longest at Jaumave, generally shortest at Orizaba and Aljojuca, and again somewhat intermediate at Palitla, although the measurements do not overlap those at Jaumave; (4) body depth varies greatly, in part because of the reproductive condition of the female, as at Aljojuca (see below); (5) head length shows little or no sexual dimorphism at Aljojuca, Orizaba, or in the Río Atoyac at Atoyac (10 males, 269-283, ave. 273, 10 females, 260-280, ave. 269), but is dimorphic at Palitla and Jaumave (and might be found to be so in populations at lower elevations between Atoyac and Palitla); (6) snout length is sharply dimorphic between the sexes at all four localities, as are predorsal length and distance between dorsal origin and base of caudal fin; but that (7) the distance from anal origin to caudal base is neither sexually dimorphic nor significantly different in the four samples.

The number of dorsal-fin rays is highest at Jaumave, among the lowest at Aljojuca, and intermediate at Palitla (Table 2).

Vertebral number is rather consistently 32, varying from 31 to 33, in Puebla and adjoining parts of Veracruz, but shows a decrease toward the north (southwest of Poza

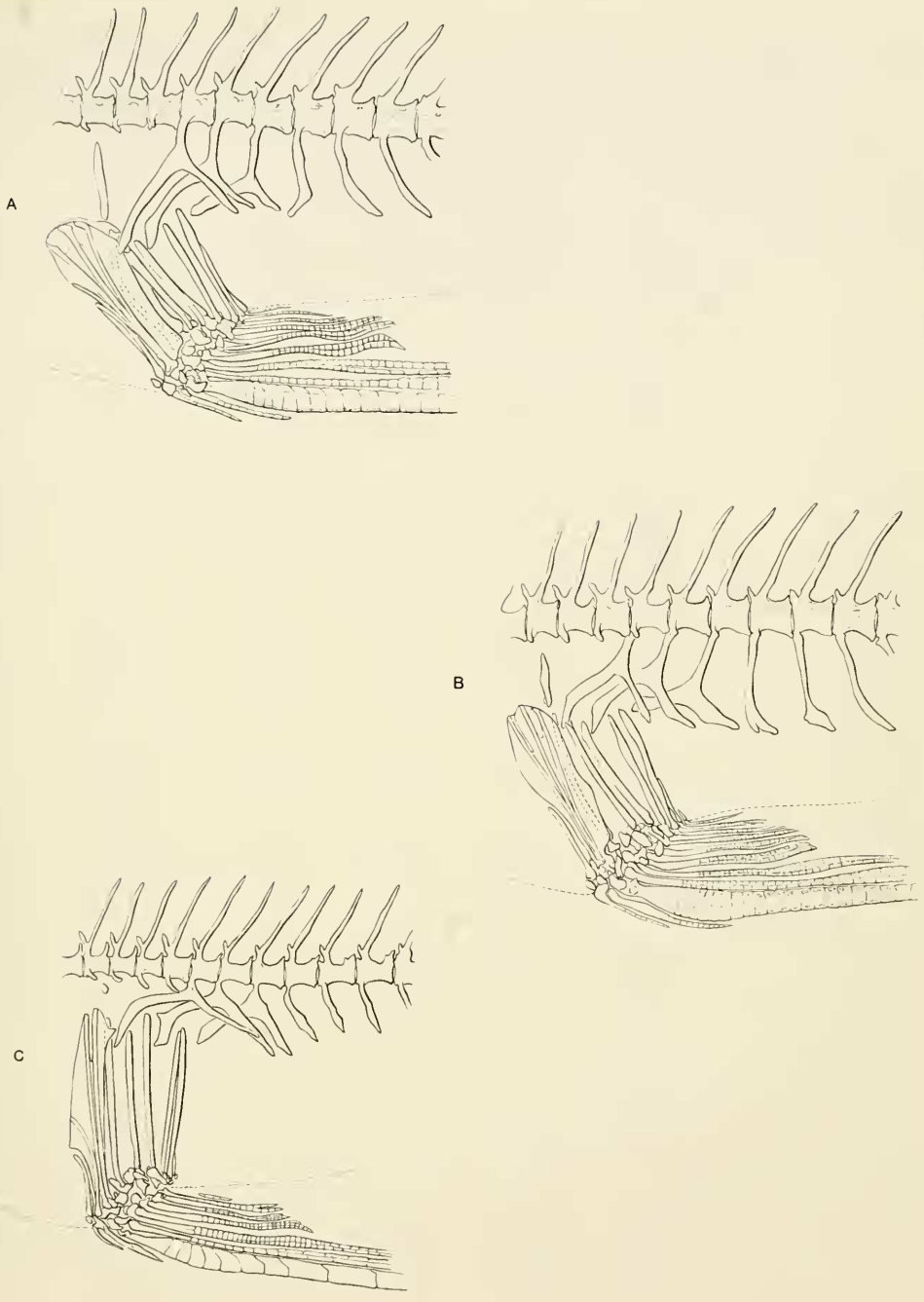

Figure 3. Gonopodial suspensoria of: A. *Heterandria jonesi*; B. *Heterandria bimaculata*; C. *Heterandria formosa*. (From same specimens illustrated in Fig. 2.)

Rica, in the Río Cazones basin), especially at Jaumave, where the mode is 31 and the range 30 to 32 (Table 4).

Color pattern is rather consistent for the populations from the Puebla Plateau (Alojojuca, Tepeaca, Acosac), the Orizaba Valley, and the Río Atoyac. They are moderately to strongly barred, with 3 to 11 rather narrow and usually short, vertical bars confined to the midside from just behind the base of the pectoral fin to just before the basicaudal spot. Generally, the larger fish have the most bars. These vary from 5 to 9 in the

Table 3. Proportional measurements of *Heterandria jonesi* and *H. bimaculata* (in permillage of standard length).

	Heterandria jonesi				*H. bimaculata*	
	Aljojuca P 203	Orizaba 183894	Palitla 162141	Jaumave 183887	Córdoba 108614+ 181309	Cosolapa 183902
Standard length, Range (mean) No.						
Males	23.0-36.1 (27.2) 7	23.6-36.1 (30.9) 15	24.4-37.1 (30.1) 14	22.8-27.1 (25.4) 7	30.1-48.4 (38.9) 15	25.5-51.9 (39.2) 15
Females	31.1-41.6 (38.2) 4	29.9-55.5 (41.5) 15	30.1-55.0 (38.9) 13	26.0-47.1 (36.7) 15	32.7-68.4 (50.0) 15	43.1-76.2 (55.9) 15
Body depth						
Males	267-290 (282)	264-295 (280)	264-297 (281)	266-306 (293)	253-290 (270)	249-288 (267)
Females	255-283 (267)	274-333 (299)	271-296 (282)	296-323 (310)	240-281 (261)	248-281 (265)
Predorsal length						
Males	516-534 (525)	500-538 (516)	489-532 (519)	498-522 (510)	453-494 (470)	452-486 (470)
Females	575-593 (587)	568-597 (582)	553-573 (563)	561-589 (576)	496-536 (520)	516-546 (528)
D. Origin to C. base						
Males	490-518 (500)	495-520 (507)	492-531 (515)	515-533 (523)	540-583 (563)	539-571 (554)
Females	421-430 (426)	427-461 (445)	456-483 (466)	450-476 (462)	477-514 (500)	479-508 (493)
A. origin to C. base						
Females	437-453 (445)	413-452 (437)	431-448 (439)	422-450 (437)	431-470 (455)	438-460 (449)
Head length						
Males	270-287 (279)	263-280 (269)	263-296 (278)	266-276 (270)	266-287 (276)	250-275 (261)
Females	270-286 (279)	263-293 (277)	276-308 (295)	272-300 (284)	252-306 (281)	252-282 (267)
Snout length						
Males	78-89 (83)	78-87 (82)	86-96 (92)	79-82 (81)	85-100 (92)	82-96 (89)
Females	93-97 (95)	92-105 (98)	99-111 (105)	92-103 (98)	89-108 (102)	94-107 (101)
C. peduncle depth						
Males	163-177 (170)	158-176 (168)	148-186 (169)	166-193 (184)	165-186 (178)	157-190 (178)
Females	147-151 (150)	144-161 (151)	160-171 (164)	172-183 (176)	155-178 (162)	153-168 (161)
D., basal length						
Males	235-255 (244)	225-256 (245)	268-299 (284)	302-325 (309)	326-369 (348)	329-358 (342)
Females	205-210 (207)	202-226 (213)	242-267 (253)	264-290 (274)	284-310 (300)	273-315 (302)
A., depressed length						
Females	190-203 (196)	182-211 (196)	203-225 (213)	234-252 (244)	193-239 (212)	199-243 (220)
C., length middle rays						
Males	238-258 (248)	221-245 (232)	237-275 (258)	279-289 (283)	227-260 (239)	231-275 (248)
Females	220-227 (223)	206-231 (215)	225-256 (246)	257-284 (271)	203-239 (218)	201-230 (216)

material examined from Aljojuca, although large females (such as the syntype figured by Regan, 1906-08: pl. 12, fig. 8, 65 mm S.L., examined by me) may show no trace of bars. At Acosac, adults of both sexes have from 3 to 8 bars, although a 63-mm female lacks

them. In the Orizaba Valley, 45 fish (30 males, 15 females) have from 4 to 10 bars. Vertical bars are most strongly developed in the two samples from Río Atoyac, wherein all fish (including young only 11 mm long) are barred, and the number of bars varies in 53 adults from 6 to 11, usually 8 to 10. In the Río Cazones drainage (42 km WSW of Poza Rica), the bars on males are weakly developed (1-7 in 14) and are apparently lacking in females and juveniles. At Palitla, bars are also weakly developed in males (from none to 7) and none is evident in females or juveniles. The extreme variation is attained at Jaumave, where none of the fish collected show vertical bars. The basicaudal spot, also quite uniform from the Puebla Plateau to Río Atoyac, is rather small, generally oval, and lies mostly on the base of the caudal peduncle not far above the body axis (Fig. 1). In the Río Cazones collection, the spot is larger, higher, and almost as much of it lies on the caudal fin as on the peduncle, thus more closely approaching the basicaudal spot typical of *H. bimaculata*. At Palitla, the spot is more like that at Río Atoyac except that it lies higher above the body axis. At Jaumave, the basicaudal spot is similar to that at Palitla but tends to become obsolete in large females.

Biology.—As suggested above, body depth in females is strongly influenced by pregnancy. In the four mature females measured from Aljojuca (Table 3), collected 21 May 1949, there were large mature eggs but no embryos. Permillage values for body depth are from 255 to 283 (avg. 267), whereas in 43 females from the three other localities (with mean standard lengths not greatly different from those of the females from Aljojuca) these values are from 271 to 333 (avg. 282, 299, 310). Clearly the reproductive season is much shorter at Aljojuca (2,385 m) than it is at the lower elevations. For example, in the 10 largest and fattest females, collected 18 March 1968 from Acosac (UMMZ 183986, ca. 1,830 m), one had advanced embryos, one had early embryos, and eight were packed with large eggs—demonstrating that at this lower elevation the reproductive season was well under way, even though the fish were taken earlier in the year. At still lower elevations production probably occurs over a long time span as suggested by the two collections made during the latter half of December from Atoyac (UMMZ 162143) and Palitla (UMMZ 162141), each of which contains individuals as small as 11 mm.

It is a general observation for poeciliids (but not for all viviparous cyprinodontoids—e.g., goodeids, Fitzsimons, 1972: 730) that males have determinate growth and attain maturity at widely different sizes. This is abundantly supported for *H. jonesi* by the following data giving the frequencies for each standard length measurement (rounded to nearest whole number) followed by number of specimens and mean value: Orizaba Valley (UMMZ 183894), 24 (7), 25 (16), 26 (9), 27 (9), 28 (11), 29 (8), 30 (2), 31 (4), 32 (3), 34 (6), 35 (3), 36 (2), in 80, range 23.6-36.1 mm, mean 28.1 mm; Rio Atoyac at Atoyac (UMMZ 183896), 27 (1), 29 (1), 30 (1), 31 (2), 32 (1), 35 (1), 36 (2), 37 (7), 38 (3), 39 (2), 41 (1), 42 (1), 45 (1), 46 (1), 25, 37.5 (range 27.5-45.7 mm). The Orizaba collection is from a spring-fed, roadside ditch, whereas the Atoyac collection is from a large river.

At only one locality and at only one time were *H. jonesi* and H. *bimaculata* taken together and then the circumstances were unusual although the data on number of dorsal rays suggest that sympatry may be normal in this area. The collection was made by W. McLane and B. Schultz on 23 December 1940 in the Río Atoyac (then in flood), 6.5 km north of Hacienda Potrero Viejo (E of Córdoba and N of Hwy 150) and contains 96 specimens of *H. jonesi* (11-53 mm, UMMZ 162143), including one transforming male, and 38 of *H. bimaculata* (10-40 mm, UMMZ 162144), including one mature male. The dorsal rays (Table 2) show an overlap only at 13 rays; the 8 specimens of *H. bimaculata* with that number are discussed under Variation in the account of that species.

Range.—The northern limit of this species (Fig. 4) is the Río Guayalejo of southeastern Tamaulipas, the major tributary of the Río Tamesí, where it must be scarce. Darnell (1962) failed to take *Heterandria* in the 66 collections (totaling over 11,000 fishes) made during 1950-53 in the Tamesí basin, and that only two collections are known from that drainage: 2 specimens from near the bridge just west of Nuevo Morelos, Tamaulipas, Rosen and Gordon, 18 January 1957 (specimens lost), and 94 from Jaumave, discussed herein. The species is probably widespread in suitable habitats throughout the Río Pánuco basin (up to elevations near 2,000 m—e.g., Tula, Hidalgo) southward to the Río

Table 4. Number of vertebrae in three species of *Heterandria* from México and Florida.

Species, cat. no.[1], locality	Number of vertebrae					No.	Avg.
	30	31	32	33	34		
H. jonesi (México)[1]							
P 203, L. Aljojuca, Puebla (topotypes)	–	–	12	2	–	14	32.14
P 184, Tepeaca, Puebla (Balsas basin)	–	2	8	–	–	10	31.80
183986, Acosac, Puebla (Balsas basin)	–	–	13	–	–	13	32.00
187718, Orizaba Valley, Veracruz	–	–	19	6	–	25	32.24
183896, Río Atoyac, Atoyac, Veracruz	–	4	24	1	–	29	31.90
193493, WSW Poza Rica, Veracruz (Cazones basin)	–	11	6	1	–	18	31.44
162141, Palitla, S.L. Potosí (Pánuco basin)	–	4	22	–	–	26	31.85
183887, Jaumave, Tamaulipas (Tamesí basin)	5	24	1	–	–	30	30.87
H. bimaculata (México)[1]							
USNM 31023, 45489, Mirador, Veracruz (Chachalacas basin)	–	1	13	–	–	14	31.93
108614, 181309, Córdoba, Veracruz (subtopotypes)	–	–	13	17	–	30	32.73
183902, Cosolapa, Oaxaca (Papaloapan basin)	–	–	12	7	1	20	32.45
124234, near El Hule, Veracruz (Papaloapan basin)	–	8	8	–	–	16	31.50
178533, Río Sarabia (Coatzacoalcos basin)	–	3	20	1	–	24	31.92
H. formosa (Florida)							
USNM 133265, Crows Bluff, Deland, males	–	–	2	12	1	15	32.93
females	1	7	9	–	–	17	31.47
USNM 210703, Monroe Station, Tamiami Trail, males	–	–	6	14	2	22	32.82
females	–	6	9	1	–	16	31.69

[1]All catalogue numbers are UMMZ, except as noted. Localities under *H. jonesi* are arranged from high to low elevations (Aljojuca to Atoyac) and from south to north (Poza Rica to Jaumave); under *H. bimaculata*, they are arranged from north to south.

Nautla. The species reappears in the Río Atoyac, southwest of Veracruz (City), and is the only *Heterandria* of the Orizaba Valley and the streams, irrigation ditches, and crater lakes (Aljojuca only) of the Puebla Plateau, where it occurs as high as 2,385 m. In this elevated region it lives in tributaries of the Río Balsas and Río Papaloapan as well as in waters without exit to the sea. Its distribution south of the latitude of Tehuacán (1,649 m) is unknown, but it has not been found in the lowlands of the Papaloapan basin or anywhere in the Río Coatzacoalcos system, the next major drainage to the south.

Zoogeography.—The occurrence of *Heterandria jonesi* in a high-elevation crater lake (Aljojuca) in the endorheic, semidesert basin (area ca. 8,000 km^2) occupied by the Llanos de Puebla or San Juan (Tamayo, 1964: 113, Fig. 4) calls for explanation. The remnant native fish fauna (*Chirostoma, "Poblana"*, and *Heterandria*) in this area indicates that the interior basin they now occupy was connected with at least three different major drainages during late Cenozoic time. Barbour (1973) has presented convincing biological evidence to tie the area in with the Río Lerma basin via the Valle de México. The occurrence of the cyprinid *"Aztecula vittata* (Girard)" in Pleistocene lake deposits and an adjacent Recent tributary of the Balsas basin just south of the city of Puebla (Miller and Uyeno, MS) demonstrates a former connection between the Valle de México, Llanos de San Juan, and the Río Balsas drainage. Finally, the occurrence of the otherwise exclusively Atlantic (in México) subgenus *Pseudoxiphophorus* in both Lago de Aljojuca and in Río Balsas tributaries proclaims a former connection between the Llanos de San Juan, the Atlantic slope, and the Balsas system.

Why does not *Heterandria jonesi* also occur in the three other fish-inhabited crater lakes and in Laguna de El Carmen (the large marsh-like, shallow lake just west of the crater lakes)? Probably because those lakes contain species of atherinids that either prey on the newborn young of the poeciliid or outcompete *Heterandria* in other ways. Lago de Aljojuca contains only *Heterandria* which elsewhere in this plateau region occurs only in

spring-fed ditches and ponds that contain no other fishes.

Alvarez (1972) has presented the following hypothesis to explain the distribution of the fishes of the Llanos. Prior to the Pleistocene this plateau region contained an enormous shallow lake that was connected to the Valle de México by way of Apizaco and Apam (Barbour, 1973: Fig. 5). The crater lakes in question were formed much later by volcanic explosion, and their cavities were filled with water because they all lay below the highest level of the Plio-Pleistocene lake. Because of their different altitudes, the crater lakes were isolated from each other at varying times as the level of the hypothetical lake fell below 2,440 meters.

Lago de Aljojuca is the highest of these fish-supporting crater lakes and some particular aspect of the history of its colonization, as yet undetermined, must account for the fact that it alone contains *Heterandria*. Very likely other species of fishes became extinct in the area following virtual desiccation of the original lake.

Specimens examined (All in México).— Hidalgo: M74-48, in UMMZ, ditch near Tula; Puebla: BMNH 1873.1.13.1 (syntype), Lago de Aljojuca; P 184 (10), Tepeaca; P 203 (20 topotypes), Lago de Aljojuca; UMMZ 124304 (47), Río Necaxa; UMMZ 183986 (50), trib. Río Balsas at Acosac; UMMZ 186675 (57), trib. Río Papaloapan, Tehuacán; UMMZ 193493 (19), trib. Río San Marcos, 42 km WSW of Poza Rica. San Luis Potosí: UMMZ 124330 (48), 162141 (45), Palitla; Tamaulipas: UMMZ 183887 (94), Jaumave. Veracruz: UMMZ 162143 (96), Río Atoyac, 6.5 km N Potrero Viejo; UMMZ 183894 (500), Orizaba Valley; UMMZ 183896 (869), Rio Atoyac at Atoyac; UMMZ 187718 (476), Orizaba Valley.

Heterandria bimaculata (Heckel)
(Figs. 1-3)

Xiphophorus bimaculatus.— Heckel, 1848: 297-299, pl. 9, figs. 1-2 (original description; a clear brook of the Orizaba Mountains, México).

Poecilioides bimaculatus.— Steindachner, 1863: 176 (original description; Teapa, Tabasco, México — see Rosen and Bailey, 1963).

Pseudoxiphophorus bimaculatus.— Garman, 1895: 81-82, pl. 3, fig. 6, pl. 8, fig. 9 (in part; synonymy; description). Meek, 1902: 98 (brief description; maximum adult size; notes on eggs, embryos, time of birth). Meek, 1904: 127-128 (in part; synonymy, excluding *P. pauciradiatus* Regan; description; range). Regan, 1904: 256 (comparison with *P. pauciradiatus*; *P. reticulatus* Troschel in synonymy). Regan, 1913: 993-994, fig. 170C (synonymy; description; gonopodium figured). Scrimshaw, 1946 (size of ova and ovisac). Rosen and Gordon, 1953: 26, Fig. 32C (gonopodium). Rosen and Mendelson, 1960: fig. 4M (hypothetical correlation between sensory canals of head and feeding habits). Rosen and Tucker, 1961: fig. 2 (secondary sex characters and sexual behavior).

Heterandria bimaculata.— Rosen and Bailey, 1963: 131, figs. 49B, 51D, 55B (in part; synonymy, excluding references to *jonesi* and *pauciradiatus*; range; skeleton and gonopodial suspensorium of male figured). Miller, 1966: 790 (range).

Gambusia bimaculata.— Regan, 1906-08: 98, pl. 14, fig. 4 (synonymy; description; range, excluding Orizaba).

Gambusia (*Pseudoxiphophorus*) *bimaculata*.— Regan, 1907: 260 (listed in comparison with *G. annectens*).

Pseudoxiphophorus bimaculatus bimaculatus.— Hubbs, 1924: 18 (synonymy; distribution; dorsal-ray counts).

Pseudoxiphophorus bimaculatus taeniatus.— Regan, 1905: 363 (original description; San Domingo de Guzman, Oaxaca, México; this locality, now called Petapa, is on a tributary of the Río Coatzacoalcos SW of Matías Romero).

Pseudoxiphophorus bimaculatus peninsulae.— Hubbs, 1936: 230-232, pl. 8, fig. 1 (original description; vicinity or Progreso, Yucatán, México).

Pseudoxiphophorus reticulatus.— Troschel in von Müller, 1865: 638-639 (original description; México).

Diagnosis.—A species of the subgenus *Pseudoxiphophorus* (Table 1) distinguished from *H. jonesi* as follows (see also Table 5): Terminal segment of ray 4a of gonopodium greatly elongate (as long as 4-8 subdistal segments), its tip strongly hooked forward (J-shaped), reaching tip of enclosing membrance; anterior margin of 4 to 6 subdistal segments of ray 4a with keel-like prominences; ray 4p not entering into curved tip of gonopod (Fig. 2). Base of dorsal fin enters predorsal length 1.2 to 1.5 times in males, and 1.6 to 1.9 times in females. Origin of dorsal fin more anterior (Table 3). Basicaudal spot generally larger, higher, and more posterior, lying mostly on caudal fin.

Type Locality.—Confusion has resulted from the common misinterpretation of Heckel's type locality as "Orizaba". In the same paper in which *H. bimaculata* is described, Heckel (1848) also described *Xiphophorus helleri* and *Poeciliopsis gracilis* (see

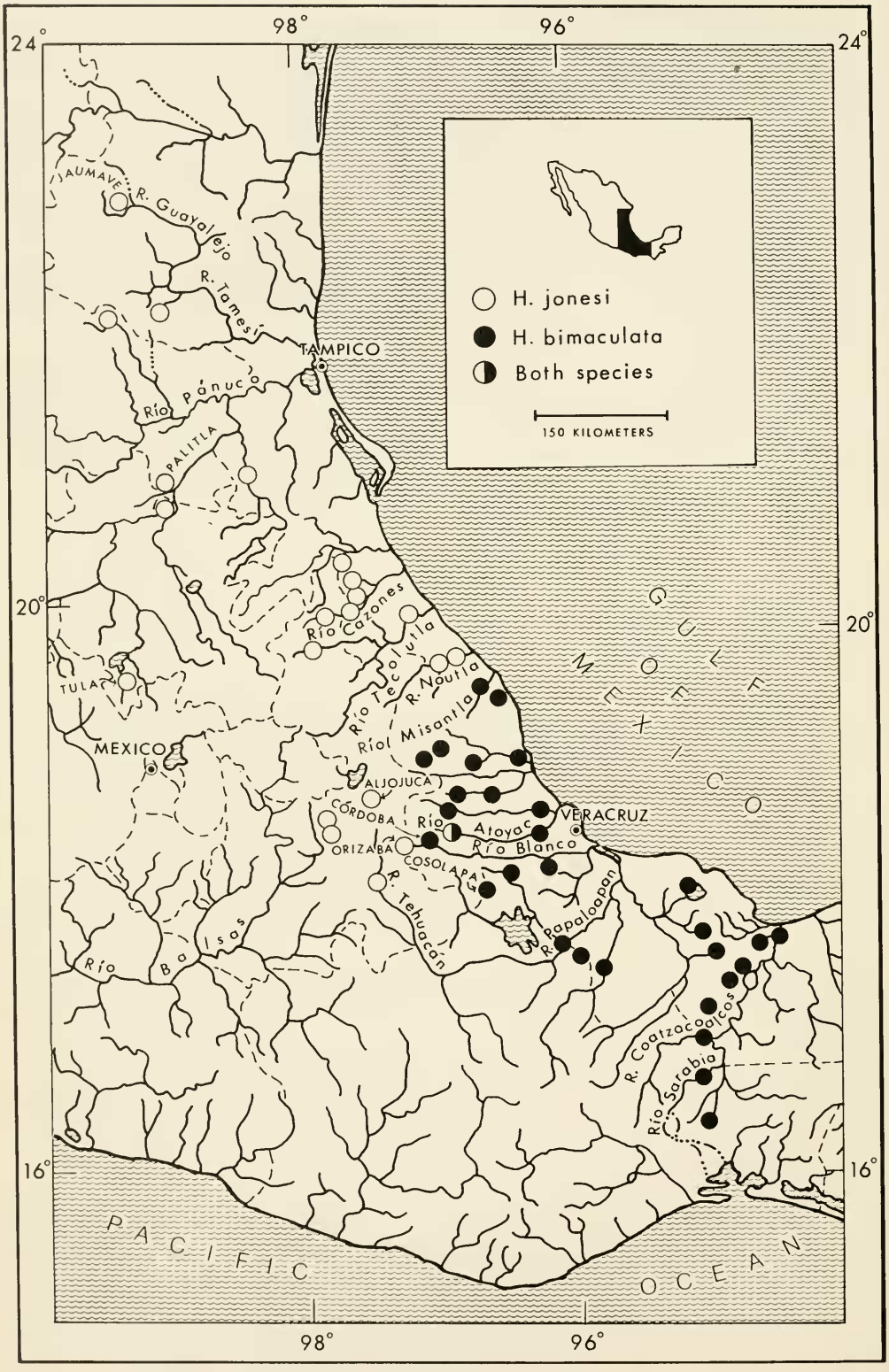

Figure 4. Distribution of two species of *Heterandria* in México. For *H. bimaculata* (which ranges eastward and southward into Nicaragua) only the records from the Río Coatzacoalcos basin northward are included. Stations are from UMMZ records and Meek's (1904: 128) localities (except Sanborn, not found).

Table 5. Comparison between two species of *Heterandria* inhabiting México.

Character	*H. jonesi*[1]	*H. bimaculata*[2]
Gonopodium (Fig. 2):		
Terminal segment of ray 4a	Short, slightly curved forward, not reaching tip of enclosing membrane; not longer than 2-3 subdistal segments, often only exceeding penultimate one	Greatly elongate, tip strongly hooked forward (J-shaped), extending to end of enclosing membrane; as long as 4-8 subdistal segments
Anterior margin of subdistal segments of ray 4a	Evenly smooth on all	With keel-like prominences on 4-6 segments
Ray 4p	Extending far beyond tip of ray 3 to form part of curved tip of gonopod	Extending just beyond tip of ray 3, not entering into curved tip of gonopod
Ray 5a	Distal part curves evenly toward tip of gonopod; ray 4p is only slightly elevated in this region	Distal part descends abruptly to ray 4p which is strongly elevated in this region
Gonopodial suspensorium (Fig. 3)	Angle of gonactinosts about 45° from vertical. Ligastyle as long as or longer than basal stem of gonapophysis III	Angle of gonactinosts about 33° from vertical. Ligastyle shorter than basal stem of gonapophysis III
Dorsal origin to caudal base	Shorter. In permillage of S.L., males 490-533; females 421-483 (Table 3)	Longer. In permillage of S.L., males 539-575; females 479-508 (Table 3)
$\frac{\text{Predorsal length}}{\text{Base of dorsal fin}}$[3]	Males 1.6-2.4; females 2.0-2.9	Males 1.2-1.5; females 1.6-1.9
$\frac{\text{Predorsal length}}{\text{Depressed dorsal-fin length}}$	Males 1.1-1.6[4]; females 1.4-2.0	Males 0.9-1.1; females 1.2-1.4
Basicaudal spot (Fig. 1)	Generally smaller, its position lower and more anterior (weakest in females from Jaumave)	Generally larger, its position usually higher and more posterior
Cross-hatching on sides	Well developed and generally extending ventrally around caudal peduncle	Well developed above body axis but fading ventrally; none on venter of caudal peduncle

[1]Ratios and proportions based on specimens from 5 populations (including topotypes of *M. jonesii* and *P. pauciradiatus*) as follows: UMMZ 162141 (Palitla), 183887 (Jaumave), 183894 (Orizaba Valley), 183896 (Atoyac), and P 203 (Aljojuca).

[2]Ratios and proportions based on specimens from 2 populations (3 collections, including subtopotypes of *X. bimaculatus*) as follows: UMMZ 108614 and 181309 (Córdoba), and 183902 (Cosolapa).

[3]This ratio was determined mathematically by dividing the measurement of the base of the dorsal fin into that of the predorsal length for each fish.

[4]The ratio of 1.1 in *H. jonesi* occurred in only 1 male from Jaumave; otherwise the range was 1.2-1.6.

Rosen and Bailey, 1963: 131-133) and stated that all three species live together "in einem klaren Bache des Gebirges Orizaba". Although *X. helleri* inhabits streams of the Orizaba Valley, neither *H. bimaculata* nor *P. gracilis* live there (the only other known fish is *H. jonesi*). Therefore, apparently none of Heckel's species came from any tributary of or stream in the trough-like Orizaba Valley, which lies at an elevation of about 1,240 m. Menzel and Darnell (1973: 232), in discussing the type locality of *Poecilia mexicana* Steindachner, also said to be from Orizaba, concluded that the types came from a much lower elevation in either the Río Jamapa or Río Blanco drainages. Most likely *X. helleri* and *H. bimaculata* (if not *P. gracilis*) came from the vicinity of Córdoba at an elevation of about 870 m. Woolman (1894: 65) described the rapids and barrier falls in the Río Blanco, the drainage system of the Orizaba Valley, which prevent the ascent of fishes into

this valley from lower elevations to the east of Orizaba.

Variation.—The salient characters distinctive of the gonopodium of this species have been given in the Diagnosis and also appear in Table 5. Additional traits follow. Ray 3 extends to the base of the penultimate segment or to that of the terminal one (the J-shaped hook) of ray 4a. Distal to the elevated flange or keel of ray 3 are from 6 to 9 small segments. Ray 4a bears from 2 to 4 squarish segments between the terminal one and the last keeled segment, and from 6 to 9 segments distal to the terminal serra on ray 4p. There are 6 to 12 segments distal to the last serra of ray 4p, and this ray bears 10 to 14 strong, retrorse serrae. Ray 5a ends several segments of ray 4a short of the base of the J-shaped hook.

Ten measurements (Table 3) were made on 30 males and 30 females sampled from two places in Veracruz and Oaxaca—Córdoba (approximate type locality of the species) and Cosolapa, approximately 50 airline km SE of Córdoba. These data show very close agreement except in head length, which is longer at Cosolapa. Sexual dimorphism is strongly marked in dorsal origin (as shown by predorsal length, and dorsal origin to caudal base) and basal length of dorsal fin; it is less striking in caudal peduncle depth and length of middle caudal rays.

The number of dorsal fin rays, lowest in the highlands (Jico-Jalapa) near the northern limit of the range, appears to show an increase southward and toward lower elevations. The extreme range for this species is from 11 to 18 (11 in one specimen from Honduras, UMMZ 173305, and 18 in three from Belize, formerly British Honduras—specimens taken by David W. Greenfield at Sta. G70-139).

Vertebral number shows modes of 32 or 33 in samples from five populations in México (Table 4).

Color pattern is generally more consistent in *bimaculata* than in *jonesi*. Cross-hatching is well developed on the upper and mid-sides but begins to pale ventrally and fades out entirely over the ventral surface of the caudal peduncle. Vertical bars are rare although Hubbs (1936: 231) stated that *H. b. peninsulae* from Yucatán has 2 to 4 such bars, "like narrow parr marks", behind the shoulder spot. Among 35 young to juvenile individuals from the Río Atoyac (UMMZ 162144) are 8 with 2 to 5 faint bars anteriorly; 7 of these have 13 dorsal rays, the number that overlaps that of *H. jonesi* at this same locality. However, in no other features do these specimens resemble *jonesi*; measurements of the basal length of the dorsal fin and predorsal length yielded calculated ratios of less than 1.0 in all eight specimens (see Table 5). Bars thus appear to be only rarely developed in *H. bimaculata*. The basicudal spot is somewhat variable in size and position. Typically it is large, roundish, more or less equal to the diameter of the eye, set higher than in *jonesi* and mostly on the caudal fin. However, in a collection from the Río Coatzacoalcos basin (Río Sarabia, Oaxaca, UMMZ 178533), the spot lies almost entirely on the base of the caudal fin, generally only slightly above the body axis, and varies from round to triangular with the apex of the triangle (often drawn out) directed posteriorly. This population (corresponding to *H. b. taeniata* of Regan) also shows a well-developed midlateral stripe that is disrupted in young specimens.

Biology.—Meek (1902: 98) reported that this species probably gives birth "near the first to the middle of June" (at Jalapa, Veracruz, 1,427 m). Possibly this is true but if so, successful fertilization and development take place later in the year than it does in *H. jonesi*. A collection (UMMZ 108614) made on 22 March from Córdoba (872 m) contains individuals as small as 14 mm standard length, indicating that brood production had been under way for some time. As already indicated (see Biology, *H. jonesi*), both species had produced young in the Río Atoyac (about 600 m) by late December.

Mature males of *H. bimaculata*, like those of *H. jonesi*, vary greatly in size: 25 (1), 27 (1), 29 (2), 30 (1), 31 (1), 32 (3), 33 (6), 34 (2), 35 (3), 37 (1), 38 (2), 39 (2), 40 (2), 43 (1), 44 (3), 45 (5), 46 (1), 47 (2), 48 (3), 49 (3), 50 (1), 51 (1), 52 (1), 48, avg. 39.4 mm (UMMZ 183902, Cosolapa). The largest of 20 immature males in this collection was 51, the smallest 40, and 16 were 41 or more mm long (all these males had the gonopodium elongated but undifferentiated at the tip). The 74 mature females in this collection, varying from 43 to 76 mm long, averaged 58.1 mm.

Sympatry between *H. bimaculata* and *H. jonesi* has already been discussed (see Biology, *H. jonesi*).

Range.—The precise northern limit of *H. bimaculata* on the Atlantic coastal plain is uncertain, but it evidently does not extend to the Río Nautla basin, which as far as known contains only *H. jonesi*. The northernmost collection known to me is from the Río Misantla (M74-6, in UMMZ; Fig. 4), an independent tributary to the Gulf of Mexico lying just southeast of the Río Nautla, Veracruz; this stream is north of Jalapa, which lies near the northernmost inland limit of *H. bimaculata*. In México the species occurs at elevations from near sea level to at least 1,430 m (Jalapa).

Specimens examined (All in México).— Oaxaca: UMMZ 178533 (52), Río Sarabia on Trans-Isthmian Hwy; UMMZ 183902 (757), Cosolapa. Veracruz: USNM 31023 (5) and 45489 (27), Mirador; UMMZ 108614 (207), Río Chico, Córdoba; UMMZ 124234 (69), 4 km E of Papaloapan (=El Hule); UMMZ 162144 (38), Río Atoyac, 6.5 km N of Potrero Viejo; UMMZ 181309 (35), Córdoba; UMMZ 184512 (94), 32.5 km N of José Cardel.

PHYLOGENY

In considering the relationships of phyletic lines within the subgenus *Pseudoxiphophorus*, it is clear from Table 5 and Figures 2 and 3 that *H. jonesi* is less specialized than *H. bimaculata*. The gonopodium, especially, is of simpler construction in *jonesi*. Although several species of this subgenus are yet to be described from Guatemala, I have examined all of them and conclude that none is more primitive than *H. jonesi*. In body form and proportions, position and size of the dorsal fin, head shape, length of mandible, and detailed architecture of the gonopodium, each of the Guatemalan species shows some features that indicate a less generalized condition than is found in *H. jonesi*. The species represented by UMMZ 193893 (Alta Verapaz, Guatemala) is perhaps as close to *jonesi* as is any of the Guatemalan species, but it shows certain modifications about the distal end of the gonopodium (e.g., thickening of ray 3, increased number of small segments in ray 4a) that, to me, mark it as more specialized.

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